

Response of subarctic vegetation to transient climatic change on the Seward Peninsula in north-west Alaska

T. SCOTT RUPP,* F. STUART CHAPIN III† and ANTHONY M. STARFIELD*

*Department of Ecology, Evolution, and Behaviour, University of Minnesota, St. Paul, MN 55108, USA, †Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99775, USA

Abstract

Understanding the response of terrestrial ecosystems to climatic warming is a challenge because of the complex interactions of climate, disturbance, and recruitment across the landscape. We use a spatially explicit model (ALFRESCO) to simulate the transient response of subarctic vegetation to climatic warming on the Seward Peninsula (80 000 km²) in north-west Alaska. Model calibration efforts showed that fire ignition was less sensitive than fire spread to regional climate (temperature and precipitation). In the model simulations a warming climate led to slightly more fires and much larger fires and expansion of forest into previously treeless tundra. Vegetation and fire regime continued to change for centuries after cessation of the simulated climate warming. Flammability increased rapidly in direct response to climate warming and more gradually in response to climate-induced vegetation change. In the simulations warming caused as much as a 228% increase in the total area burned per decade, leading to an increasingly early successional and more homogenous deciduous forest-dominated landscape. A single transient 40-y drought led to the development of a novel grassland–steppe ecosystem that persisted indefinitely and caused permanent increases in fires in both the grassland and adjacent vegetation. These simulated changes in vegetation and disturbance dynamics under a warming climate have important implications for regional carbon budgets and biotic feedbacks to regional climate.

Keywords. boreal forest, climatic change, landscape dynamics, spatially explicit, transient dynamics, treeline

Received 11 April 1999, resubmitted 2 November and accepted 30 November 1999

Introduction

Vegetation response to climatic warming could feed back to cause large changes in regional and global climate through effects on terrestrial carbon storage (Smith & Shugart 1993) and on water and energy exchange (Charney *et al.* 1977, Bonan *et al.* 1992; Chapin & Starfield 1997). The rate and magnitude of this feedback is influenced by transient changes in the distribution of terrestrial ecosystems in response to changes in climate, disturbance regime, and recruitment rates. The long-term direction of ecosystem change is also sensitive to spatial patterns and processes operating at the landscape scale (Turner *et al.* 1994, 1997; Fastie 1995).

Current predictions of vegetation response to climatic warming assume either disturbance regime does not change (Pastor & Post 1988; Sirois *et al.* 1994) or use globally averaged rates of disturbance (Smith & Shugart 1993). Conversely projections of future disturbance regime in a warmer climate (Flannigan & Wagner 1991; Kasischke *et al.* 1995; Flannigan *et al.* 1998, Gardner *et al.* 1999) generally neglect rates and patterns of vegetation response to climate and disturbance. However, the climate–disturbance–vegetation interactions clearly influence the rate and pattern of changes in vegetation (Neilson 1993; Noble 1993) and disturbance (Gardner *et al.* 1996) through effects on fire probability and spread (Gardner *et al.* 1999), and pattern of colonization (Turner *et al.* 1997).

Landscape-scale interactions between vegetation and disturbance are particularly important at the forest–

Correspondence: T. Scott Rupp, Forest Soils Laboratory, University of Alaska, Fairbanks, AK 99775, USA, fax +1/907-474-6184, e-mail psulions@alaska.net

tundra ecotone (Noble 1993; Starfield & Chapin 1996; Chapin & Starfield 1997), where vegetation change will have large feedbacks to climate (Pielke & Vidale 1996). The predicted colonization of tundra by forest will likely increase terrestrial carbon storage (Prentice & Fung 1990, Smith & Shugart 1993), reducing the warming potential of the atmosphere, and increase absorption of solar radiation (Bonan *et al.* 1992, Thomas & Rowntree 1992, Chalita & Le Treut 1994; Foley *et al.* 1994) creating a positive feedback to regional warming (Chapin & Starfield 1997).

Modelling transient dynamics of vegetation change allows investigation of both the short- and long-term responses of ecosystems to landscape-level disturbance and recruitment, and the subsequent feedbacks between climate and the biosphere. These spatial processes are responsible for long-term changes in vegetation distribution (Dale 1997) in response to changing climate and must eventually be incorporated into large spatio-temporal scaled models of gradual climatic change. In this paper we use a spatially explicit model (Rupp *et al.* 2000) that simulates the response of subarctic vegetation to climatic warming. We investigated the sensitivity of vegetation change on the Seward Peninsula in north-west Alaska to different rates of climatic change over a 500-y period.

Methods

Study site

Model simulations were conducted in north-west Alaska on the Seward Peninsula (the simulation landscape measured 200 × 400 km) (Fig. 1a). The area was selected because it includes a climate/vegetation gradient from upland tundra to treeline, and therefore might undergo considerable vegetation change in a warming climate. Currently, the landscape is dominated by tundra (either treeless tundra or tundra with some level of spruce canopy present) with a small proportion of spruce forest, which increases as one travels inland. Elevation ranges from sea level to 2200 m, but most of the landscape is less than 600 m. Fires are infrequent, due to the low density of lightning strikes (Reap 1991) and burn primarily in tundra (the dominant vegetation type on the Seward Peninsula). Most fires in Alaska are stand-replacing fires that leave a mosaic of burned and unburned patches on the landscape (Vioreck 1973).

Climate on the Seward Peninsula is characterized by long cold winters (−20° to −30 °C) (Hammond & Yarie 1996). The growing season (May–Sept.) is cool and wet along the coast, with warmer and drier conditions inland. Growing-season precipitation accounts for about 60% of the annual total and increases by two-fold from

north to south. Snowfall patterns show a similar N–S trend, with mountains receiving twice the amount of lower elevations. Current climate records (1950–98) for Nome (a coastal weather station) show average annual growing-season temperatures (May–Sept.) ranging from 5° to 9 °C (mean of 7 °C), and total growing-season precipitation ranging from 146 to 450 mm (mean of 247 mm). Average annual precipitation is 405 mm. Average annual snowfall is 150 cm, with only 8 cm falling during the growing season (95% falling in early May).

Model overview

ALFRESCO (Alaskan Frame-based Ecosystem Code) simulates the response of subarctic vegetation to transient climatic change in Alaska (Rupp *et al.* 2000). The model assumptions reflect our hypothesis that fire regime and climate are the primary drivers of landscape-level changes in the distribution of vegetation in the circumpolar arctic/boreal zone (Payette 1983; Van Cleve *et al.* 1991; Bliss & Matveyeva 1992; Holling 1992; Starfield & Chapin 1996). Assuming a warming climate we expect tundra to change to forest (Pastor & Post 1988; Hobbie & Chapin 1998) and the frequency and extent of fires to increase (Flannigan & Wagner 1991, Stocks 1991; Kurz & Apps 1995) over the time-period spanning the next decades to centuries.

ALFRESCO operates at a 10-y time-step, the average frequency of severe fire years in the North American boreal forest (Flannigan & Harrington 1988), and calculates vegetation change in a landscape composed of 2 × 2 km pixels, a scale appropriate for interfacing with mesoscale climate models (Starfield & Chapin 1996). The model was initially developed and parameterized for upland tundra and forests of Alaska as a nonspatial model (Starfield & Chapin 1996), which was later made spatially explicit to improve its representation of the spatial processes of fire spread and seed dispersal (Rupp *et al.* 2000).

The model simulates four major subarctic ecosystem types: upland tundra, white spruce forest, deciduous forest, and grassland-steppe. The grassland ecosystem type is currently not a large component of the subarctic boreal forest, except for local occurrence on dry south-facing slopes (Yurtsev 1982, Lloyd *et al.* 1994), but was widespread during the late Pleistocene (Hopkins *et al.* 1982; Zimov *et al.* 1995) and occurs regularly in the southern reaches of the boreal forest (Hogg & Hurdle 1995). The ecosystem types represent a generalized classification of the complex vegetation mosaic characteristic of the circumpolar arctic and boreal zones (Solomon 1992; Starfield & Chapin 1996; Rupp *et al.* 2000).

ALFRESCO is a frame-based model (Starfield *et al.* 1993), where each ecosystem type (i.e. frame) constitutes an independent submodel. Each submodel calculates and monitors factors and processes that could cause a switch to another ecosystem type. Switching rules establish whether a switch from one frame to another occurs, deactivating the current submodel and activating the submodel representing the new ecosystem type. This approach emphasizes processes causing vegetation change, not variables controlling productivity or species composition within a vegetation type, as developed in gap dynamics models (Shugart & West 1980; Pastor & Post 1986; Starfield & Chapin 1996). Thus, during the development of the original nonspatial model, a number of parameters and processes (e.g. soil fertility, soil moisture, permafrost depth and shrub biomass) were investigated for inclusion in the model, but were excluded because they influence within-stand dynamics more strongly than the nature and timing of switches among ecosystem types (Starfield & Chapin 1996).

The model uses both quantitative and qualitative variables, an innovative technique employed by frame-based models (Starfield 1991; Starfield *et al.* 1993). Quantitative variables are employed where actual numbers seem appropriate (e.g. age-dependent mortality rates). Qualitative variables and rules are used to describe general ecological relationships, where data are limited or detail is unnecessary (e.g. seed availability) (Starfield & Chapin 1996).

Model input data were generated from GIS raster coverages, within the GRID environment of ARC/INFO (ESRI 1994). The data came from Alaskan datasets of current growing-season temperature and precipitation (Hammond & Yarie 1996), current vegetation (Fleming 1997), and topography. Elevation data were created from 15-minute Alaska digital elevation models (USGS 1990). ASCII input files were generated from the spatial datasets and read into the initialization routine of the model.

Climate

ALFRESCO generates climate stochastically based upon observed (1960–90) growing season (May–Sept.) climate in Alaska (Hammond & Yarie 1996). Climate is input to the model as a series of 10 alternative maps of growing-season temperature and precipitation. These maps have a geographical pattern of climate that is logically consistent with topography and latitude (e.g. colder in mountains and to the north) and with observed synoptic climatology (e.g. more precipitation near coastal moisture sources). The climate maps preserve these basic geographical patterns of climate, but differ in the magnitude of temperature and precipitation. The temperature maps

range from -2°C colder to $+7^{\circ}\text{C}$ warmer than current climate. Precipitation maps were derived from projections of future Alaskan climate by four GCM's (Maxwell 1992; Chapin & Starfield 1997). From these projections, precipitation maps were uniformly increased (or decreased for colder temperature maps) by 15% for each 1°C change from the observed current average temperature.

The actual maps of temperature and precipitation chosen at each time-step are selected in two stages. First, a climate scenario is chosen (e.g. current climate or $+2^{\circ}\text{C}$ instantaneous change). Then, for each climate scenario there is an associated probability distribution of choosing a particular map of temperature and of precipitation for a given time-step. These frequency distributions (around growing-season mean values) of both current temperature and precipitation were developed from climate records for a tundra site (Nome), a treeline site (Haugen 1982), and a boreal forest site (Fairbanks) (Starfield & Chapin 1996; Chapin & Starfield 1997). Precipitation and temperature maps are chosen independently at a given time-step (i.e. a 1°C temperature increase does not necessarily result in a 15% increase in precipitation). For example, under current climate, the map that represents the observed average growing-season temperature (1960–90) has a 60% chance of being chosen (in any given time-step), while the observed precipitation regime has only a 40% chance of being chosen. The temperature and precipitation in each pixel of the map is then converted to temperature and precipitation classes (1, 2, 3 or 4) that have defined effects on vegetation (Starfield & Chapin 1996; Rupp *et al.* 2000). In this way we define coherent scenarios of climatic change (e.g. instantaneous or gradual climatic warming), allow stochastic variation in temperature and precipitation at each time-step for a climate scenario, and provide geographical patterns of climate that are consistent with topography and synoptic climatology.

At each time-step, for each pixel, an 'effective drought' index (Trigg 1971; Clark 1988) class (1, 2, 3 or 4) is determined based on the temperature and precipitation class within that pixel (Table 1); the index decreases (i.e. more severe drought conditions) with increasing temperature and decreasing precipitation (Thornwaite & Mather 1957; Starfield & Chapin 1996). This index provides a measure of drought severity and is utilized in determining vegetation growth, vegetation flammability, and the probability of insect outbreak in tundra (see *disturbance* subsection). The database for probability distributions of temperature and precipitation for different climate scenarios and the relationships of climate to vegetation growth and composition, flammability, and probability of insect outbreak are presented in Starfield & Chapin (1996) and Rupp *et al.* (2000).

Table 1 Effective drought index classes (1 = driest and 4 = wettest) as determined by average growing-season temperature and total growing-season precipitation (May–September). The *Methods* section describes how the drought index affects canopy growth, vegetation flammability, and insect outbreaks

Temperature class ¹	Precipitation class ²			
	1	2	3	4
1	3	4	4	4
2	2	3	4	4
3	1	2	3	4
4	1	1	2	3

¹Class 1, < 6.5 °C, Class 2, 6.5°–9.5 °C, Class 3, 9.5°–12.5 °C, Class 4, > 12.5 °C

²Class 1, < 120 mm; Class 2, 120–180 mm, Class 3, 180–240 mm; Class 4 > 240 mm

The spatial and temporal scales in the model have important implications for the dynamics of vegetation and disturbance. For example, a 2 × 2 km pixel 'in the spruce frame' implies a vegetation mosaic in which spruce is dominant but propagules of deciduous trees and grasses are present. Similarly, at a time-step of 10 y, the growing season is not assumed to be uniformly warm or precipitation uniformly low during all 10 years. Rather, a 'cold' decade is one where there were sufficient low-temperature seasons to inhibit tree establishment, while a 'dry' decade is one where some of the years were sufficiently dry to make fires more likely.

Disturbance

The model simulates both insect outbreak (in tundra sites with spruce forest) and fire. The fire regime is simulated stochastically and is driven by climate, vegetation type, canopy cover, and time since last fire. ALFRESCO employs a cellular automaton approach, where an ignited pixel may spread to any of the eight surrounding pixels. Ignition of a pixel is determined by comparing a random number to the flammability value of that pixel. Fire spread depends on the flammability of the receptor pixel and the effect of natural fire breaks including topographic barriers (elevations > 600 m are assumed to contain little or no fuels) and large water bodies (i.e. lakes and river systems comprising the majority of a 2 × 2 km pixel). Spot fires smaller than our 2 × 2 km pixel are ignored. A 'fire' implies that more than 50% of the area burned with an intensity that killed a majority of trees. In all ecosystem types flammability is assumed to be a function of an 'effective drought' index (Trigg 1971; Clark 1988), which decreases (i.e. more severe drought

conditions) as climate becomes warmer and dryer (Thornwaite & Mather 1957, Starfield & Chapin 1996). Fire probability differs among ecosystem types due to differences in fuel build-up (e.g. vegetation type, time since last disturbance, and canopy cover) (Rupp *et al.* 2000). In this manner, we can simulate the dynamic interactions between fire, climate, and vegetation change.

Insect outbreak is currently simulated only within tundra pixels that have some spruce canopy (i.e. the forest–tundra ecotone). We assume outbreaks do not spread to neighbouring pixels and are determined by canopy cover and drought events (Mattson & Haack 1987; Holling 1992; Starfield & Chapin 1996). Insect outbreak causes a 25% reduction in tree canopy of an attacked pixel.

Seed dispersal

ALFRESCO models some forms of seed dispersal implicitly (because the sources are too small to be seen at a 2 × 2 km resolution), others explicitly. Thus the model assumes that small patches of grassland are present in pixels classified as tundra, deciduous forest, and spruce forest, so that seed is available when conditions are right for grasses to out-compete other species. Likewise scattered deciduous species are assumed to be present in spruce forest.

An increase in spruce canopy cover in tundra occurs in two ways: seed inputs from trees already present on the site (in-filling) are modelled implicitly while dispersal from outside the site is simulated in a manner similar to the fire spread routine. We assume seed dispersed from a seed source has a dispersal distance threshold of 4 km (beyond which no seed travels). Mountains (elevation > 600 m) and large water bodies physically inhibit the spread of seed. The number of neighbouring seed sources determines the amount of seed available (from outside) to a given pixel, which along with climate and in-filling determines increases in canopy cover (Rupp *et al.* 2000).

Ecosystem dynamics

The individual submodels (ecosystem types) used in ALFRESCO (a detailed description can be found at <http://www.lter.alaska.edu/pubs/alfresco.html>) are identical to those described by Starfield & Chapin (1996) and Rupp *et al.* (2000). We provide only a general overview.

Within a given submodel we simulate those mechanisms and processes that might cause a switch to a new ecosystem type. We then compare values of these parameters to thresholds defined in switching rules to determine whether a switch from one ecosystem to

another occurs. If a switch occurs, the 'old' submodel is terminated and the 'new' submodel is activated. For example, a tundra pixel may switch to spruce forest when tree canopy cover exceeds 50% or switch (with probability of 0.75), to grassland following a fire and two consecutive hot, dry decades. Tree canopy cover increases as a function of temperature and seed rain and decreases as a function of insect attack (causes a 25% reduction in canopy cover) and fire (causes a removal of all trees). The seed rain variable accounts for both infilling (seed input from established trees on the site) and dispersal from surrounding seed sources (spruce forest within 4 km of tundra). Fire and insect attack are stochastic functions of climate and tree canopy cover.

Following conversion from tundra to white spruce forest, a pixel remains forest until a fire occurs. Fire normally causes a switch to early successional deciduous forest. Deciduous forest is maintained by fire, but following a fire-free period of 90–120 years switches back to spruce forest. However, fire in association with extremes in climate may cause a switch to grassland-steppe (two consecutive hot and dry decades) or a switch back to upland tundra (two consecutive cold decades). Fire in the grassland-steppe ecosystem type causes reversion to deciduous forest or tundra, or causes the system to remain as grassland, as a function of temperature and seed availability (Starfield & Chapin 1996; Rupp *et al.* 2000).

Model simulations

The nonspatial model (Starfield & Chapin 1996) from which ALFRESCO was developed, used observations from the literature to develop fire regime parameters for each vegetation type. ALFRESCO was originally calibrated to yield similar average total area burned to that of the nonspatial model for a given vegetation type and climate regime (Rupp *et al.* 2000). The original calibration of ALFRESCO assumed that the probability of fire ignition from lightning strikes and fire spread was identical (Starfield & Chapin 1996), an assumption that worked well for a 'generalized' landscape (i.e. all of the Alaskan arctic treeline). This generalized parameterization, however, did not fit the Seward landscape. The predicted pattern of fires was skewed towards many small fires compared to the pattern of fires observed from 1950 to 1997 (Kasischke & French 1997). This discrepancy occurred because there are fewer lightning strikes on the Seward Peninsula (Reap 1991) than in the rest of interior Alaska where the original model was calibrated. We therefore recalibrated the model to match both the observed fire regime (1950–97) and the current vegetation distribution, under current climate conditions, on the Seward Peninsula.

We then simulated several different climate change scenarios (Table 2), run for 500 years, with each scenario replicated 100 times. The instantaneous warming scenarios represent the maximum rate of vegetation change that might occur under such temperature increases, whereas the ramped scenarios provide a more realistic view of future predicted climatic warming and the resultant vegetation distribution. The drought experiment simulated the effect of short-term climatic extremes on long-term vegetation distribution by imposing a 40-y drought (a climate 7°C warmer and 30% dryer than current climate) on the landscape. Past changes in Alaskan climate have often been large in magnitude (2–5°C) and duration (20–40 y) associated with changes in the Arctic Oscillation (Serreze *et al.* in press). The drought scenario we simulate is larger and longer than any recorded during the 100-y climate history of Alaska but is within the range of natural variability and therefore constitutes a useful experiment. Finally, we performed various sensitivity analyses (see results section) to identify the sensitivity of ALFRESCO to changes in model assumptions and parameter values.

Results

As described in the methods, our modelling work using a nonspatial model (Starfield & Chapin 1996) and the spatially explicit model on a hypothetical landscape (Rupp *et al.* 2000) assumed that the probability of fire ignition and fire spread were the same. This assumption produced too many small fires when applied to the

Table 2 Summary of simulation conditions for climate change experiments over a 500-y period (replicated 100 times). Instantaneous changes were initiated in the first decade. The ramped scenarios occurred continuously over 200 or 400 years and were then held constant for the remainder of the simulation

Climate experiment	Growing-season		
	Temperature increase	Precipitation increase	Type of change
1	–2°C	–30%	Instantaneous
2	No Increase	No Increase	Current climate
3	+2°C	30%	Instantaneous
4	+4°C	60%	Instantaneous
5	+2°C	30%	Ramped 200 y
6	+2°C	30%	Ramped 400 y
7	+4°C	60%	Ramped 200 y
8	+4°C	60%	Ramped 400 y
9	+7°C**	–30%	40-y drought

** expt 9 was conducted for climate scenarios in expts 1–4.

Seward Peninsula We therefore allowed fire ignition and fire spread parameters to vary independently with climate with the goal of producing simulation results that, under current climate, best matched the observed fire records between 1950 and 1997 (Kasischke & French 1997). Several parameter sets could reproduce these records. When we further assumed that the current vegetation observed on the Seward Peninsula (Fleming 1997) is in equilibrium with the current environment (i.e. observed climate and disturbance regime), there was a single parameter set that accurately simulated fire size, fire number, and vegetation composition. We used this parameter set for the remaining simulations.

The observed data for lightning strikes, fires, and climate suggested that fire spread is more sensitive to temperature and precipitation (i.e. drought index) than is ignition. Analysis of the drought index map calculated by the model for 'typical' fire weather (i.e. weather that is warmer and dryer than average observations) matched well with the location of actual fires, suggesting that our derived relationship between drought index and vegetation flammability was realistic.

Under current climate ALFRESCO simulated an average of 12 fires that burned 216 400 ha (541 pixels) per decade compared to 10 fires per decade that burned 221 200 ha (553 pixels) as observed from fire records. The model simulated an average fire size of 18 400 ha (46 pixels) compared to an observed 22 000 ha (55 pixels). ALFRESCO also simulated a steady-state equilibrium vegetation distribution that matched current vegetation, predicting (on average for 100 replicates) no change in forest cover after 500 years. This vegetation stability is consistent with the assumption that current vegetation is in equilibrium with the current climate and fire regime on the Seward Peninsula.

To further test the model we simulated the response of the landscape to a colder (instantaneous decrease of 2 °C) climate. Due to climatic constraints (i.e. growing-season temperatures too cold to support tree establishment and survival) a 2 °C decrease in growing-season temperature (average May–Sept.) reduced the amount of spruce forest on the landscape from 1.4 to 0.4% after 500 years. The cold climate prevented spruce forest destroyed by fire from being recolonized by trees, and so it remained as tundra until the end of the simulation period.

We next investigated the response of the Seward Peninsula to several scenarios of warming climate (Table 2) over the next 500 years. In all experiments, an increase in growing-season temperature caused a substantial increase in both white spruce and deciduous forest cover (Fig. 1). An instantaneous 2 °C temperature increase resulted in 15% total forest cover after 500 years, compared to 65% under a 4 °C increase (Fig. 2). The 4 °C increase also showed a greater rate of transient increase

in forest cover. In all warming scenarios the first observable change was a conversion of forest tundra (spruce canopy 1–49%) to spruce forest (Fig. 1b), followed by a combination of spruce expansion into formerly treeless tundra and conversion of spruce to deciduous forest by fire (Fig. 1c). The initial increase in forest cover lagged behind the temperature change by at least 40 years due to time required for initial establishment and growth of trees in tundra. Forest continued to expand even 500 years after the 2° and 4° instantaneous temperature increases. The ramped scenarios showed a more gradual rate of change, with total forest cover after 500 years ranging from 7% to 58% (Fig. 3). Time lags prior to initial change in forest cover were twice as long under ramped (Fig. 3) as under instantaneous (Fig. 2) temperature increases. The deciduous spruce forest ratio after 500 years changed from 1:1 (under current climate) to 4:1 (under an instantaneous 4 °C increase) (Fig. 1), reflecting changes in disturbance regime and associated successional dynamics (i.e. climax spruce forest is replaced by early successional deciduous forest following fire).

Climate warming caused a moderate increase in number of fires and a large increase in average fire size and total area burned (Fig. 4 and Table 3). These changes in fire regime occurred quickly in response to the instantaneous climatic change used in these simulations. However, the area burned continued to change throughout the simulation in response to gradual change in vegetation and landscape pattern. The initial rapid changes in area burned occurred due to climate-induced increases in the flammability of all vegetation types, which influenced the number of fire ignitions and the extent of spread. Subsequent slow changes in area burned reflected vegetation-induced increases in the overall flammability of the landscape, as more highly flammable spruce forest occupied the landscape, causing an increase in the average size of fires.

Changes in the number of fires and area burned are important landscape-level drivers of the rate and direction of succession. We investigated the influence that disturbance has on the rate and pattern of vegetation change by altering the overall level of fire activity (no-fire, halved or doubled) in the landscape under both instantaneous temperature increase scenarios (Table 4). The no-fire scenario predicted a 36% and 72% increase in total forest cover across the landscape after 500 years for the 2° and 4 °C warming scenarios, respectively, compared to 2% and 10% total forest cover for the doubled-fire scenario. With fire removed from the landscape forests consisted entirely of spruce forests, whereas the doubled fire scenario produced a deciduous-dominated forest (90–95% deciduous cover). In fact, the doubled fire scenario resulted in approximately 1% less white spruce

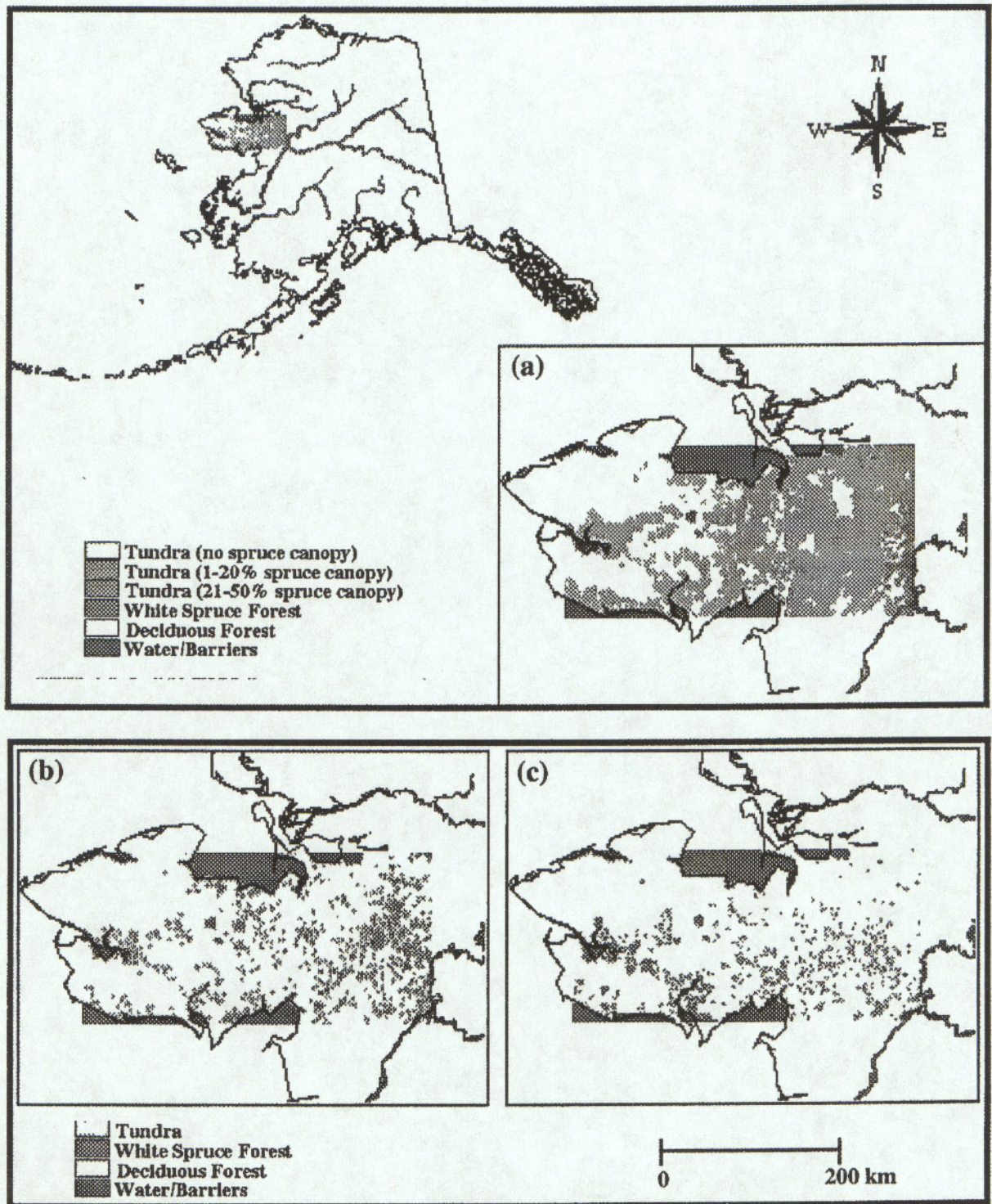


Fig. 1 Simulated response of Seward Peninsula vegetation to an instantaneous $+4^{\circ}\text{C}$ growing-season temperature increase. Maps show (a) current vegetation (b) simulated vegetation 100 y following temperature increase, and (c) 200 y following increase. The map of current vegetation stratifies tundra into 3 classes determined by the level of white spruce tree canopy cover (treeless, 1–20% cover, and 21–50% cover). The simulated response of the vegetation shows forested tundra first being converted to spruce forest (Fig 1b), followed by a combination of spruce forest expansion into tundra and conversion of spruce to deciduous forest by fire (Fig 1c)

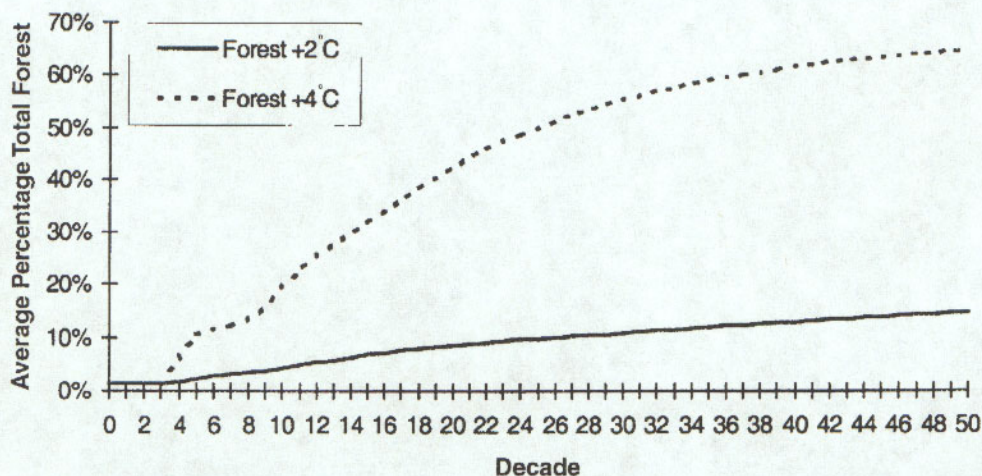


Fig. 2 Average total forest cover, both white spruce and deciduous forest, across the landscape for an instantaneous 2°C (solid line) and 4°C (dashed line) growing-season temperature increase over 500 years (replicated 100 times)

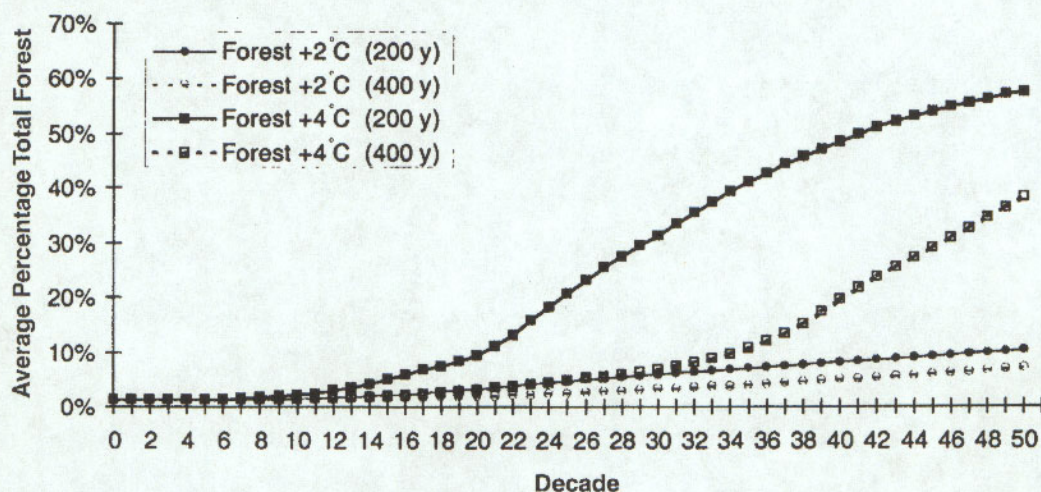


Fig. 3 Average total forest cover, both white spruce and deciduous forest, across the landscape for 2°C (grey lines) and 4°C (black lines) growing-season temperature increases ramped over 200 (solid lines) or 400 y (dashed lines). Simulated for 500 y and replicated 100 times

forest in the landscape than initially present. There appears to be a trade-off whereby a warming climate produces more favourable growing conditions for spruce forest establishment but also a more hostile environment (i.e. more and larger fires) for long-term spruce survival.

Extreme climate events can produce long-term changes in vegetation distribution and disturbance regime. We simulated a 40-y drought event 100 years into the simulation for the instantaneous -2°, +2°, and +4°C warming scenarios, as well as for current climate. Under each climate scenario a prolonged drought caused a short-term, large-scale conversion of upland tundra to dry grassland-steppe (Fig. 5a). The onset of drought initiated large fires, which burned approximately 85% of the landscape in the first decade of drought. These burns were then colonized by dry grassland in the following

decade. Grassland persisted throughout the drought due to its short fire-return interval (i.e. burns every 10 years), but a return to colder (i.e. -2°C) climate resulted in an immediate reconversion of burned grassland to upland tundra (Fig. 5b). Under current climate, there was a 130-y lag period between the end of the drought and reconversion to tundra. Under warmer climate (i.e. +2° and +4°C) grassland was either colonized by deciduous forest or persisted on the landscape (Fig. 6). The +2° scenario actually resulted in more grassland persisting on the landscape than the +4° scenario. In the +2° scenario climate was not cold enough to cause a return to tundra (i.e. as in the -2°C and current climates), but was also not hot enough to allow widespread colonization by deciduous forest (i.e. as in the +4°C scenario). This suggests grassland-steppe ecosystems under certain

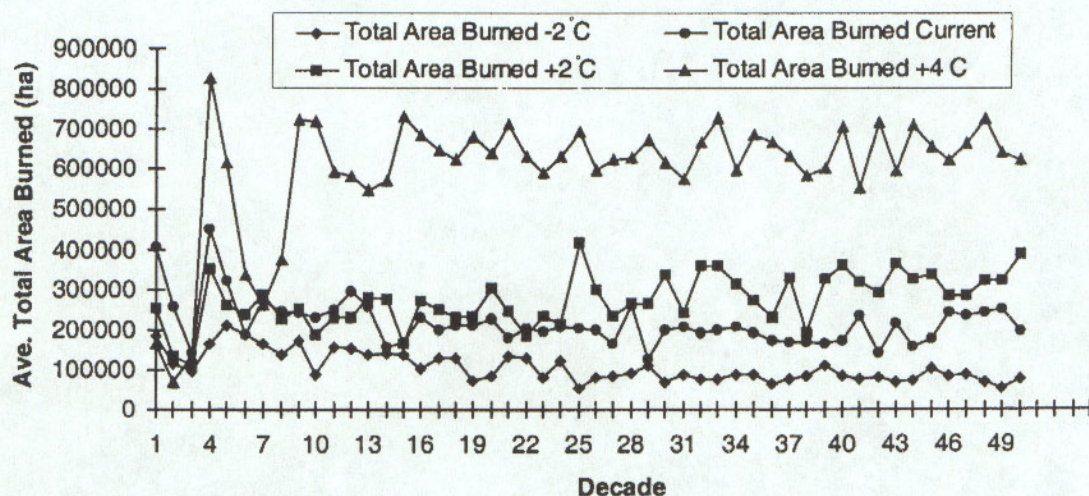


Fig. 4 Average total area burned per decade for instantaneous -2°C (diamonds), $+2^{\circ}\text{C}$ (squares), $+4^{\circ}\text{C}$ (triangles), and current climate (circles) scenarios. Simulated for 500 y and replicated 100 times.

Table 3 Summary of fire regime including average number of fires and total area burned per decade and average individual fire size for expts 1–4. Results are the average (over the 500-y simulation) for the entire landscape for 100 replicate runs

Ave./Decade	Instant -2°C	Current Climate	Instant 2°C	Instant 4°C
# Fires	11.64	11.82	12.78	15.64
¹ Area burned	106,800	216,400	273,200	597,200
¹ Fire size	9200	18,400	21,200	37,600

¹Average hectares per decade

climate conditions, once established, may remain in the landscape at relatively high levels indefinitely. Even under current climate, grassland persisted in 2% of the landscape through the 500-y simulation. Following drought a dynamic equilibrium was reached in which: (a) spruce replaced early successional deciduous vegetation over time; (b) an increase of flammable vegetation (i.e. white spruce forest) caused large fires; (c) fire-related spruce forest mortality occurred; and (d) a switch back to deciduous forest followed. This fire-vegetation feedback produced 30-y and 60-y quasi-stable oscillations in regional vegetation composition in response to 2°C and 4°C warming, respectively (Fig. 6).

Finally, we performed four sensitivity experiments to test the robustness of our results and identify the processes and factors to which ALFRESCO was most sensitive.

1 Length of drought. A 20-y drought caused the same vegetation trends as the 40-y drought (i.e. extreme short-term changes and a consistent long-term effect on vegetation). However, after a short drought a lower

proportion of total grassland remained on the landscape over time. These simulations show that in ALFRESCO, a short-term severe drought (i.e. decades in which some of the years are sufficiently dry and hot to allow for severe fires and the establishment of grassland) has long-term effects on vegetation, regardless of the length of the drought.

2 Remnant spruce trees following a fire. ALFRESCO assumes that fires in tundra kill all spruce trees. This assumption oversimplifies the complexity of fire pattern in boreal forest and likely causes a conservative estimate of potential forest response to warming. We altered the fire-effects scenario in tundra so that some remnant spruce trees (1–7%) survived tundra fires. Under current climate, this change had no effect on model results. Even under warming scenarios, the rate of conversion of tundra to spruce forest changed little, with only slightly more (1–2%) total forest (both spruce and deciduous) present after 500 years, compared to the original model assumption (i.e. all trees in tundra are killed by fire). However, this alternative model assumption did affect the fire regime (for the warming scenarios), increasing the average area burned per decade by 50 000 ha, compared to the original assumption.

3 Increased insect outbreaks. Insect outbreaks in tundra played a small role in our simulation experiments. Doubling of the probability of an insect outbreak had no effect on the model results under current climate. Under warming climate, the doubled probability of insect outbreak caused a small decrease in total forest and average area burned per decade, compared to the normal outbreak scenarios (under a warming climate). This suggests that insects could become more important agents of change in a warming climate.

Table 4 Summary of fire sensitivity experiment including average number of fires and total area burned per decade, average individual fire size, and average spruce and deciduous forest cover at the end of the simulation (initial spruce forest cover was 1.4% and deciduous forest cover was 0%). Results are the average (over the 500-y simulation) for the entire landscape for 100 replicate runs

	Spruce forest (%)	Deciduous forest (%)	¹ Area # Fires	Burned	¹ Fire size
+2 °C – No fire	36.1	0	0	0	0
+2 °C – Halved	31.3	11.1	8.5	130,368	14,779
+2 °C – Normal	14.6	9.4	12.8	273,272	21,278
+2 °C – Doubled	0.2	1.8	15.6	1,042,528	62,639
+4 °C – No fire	72.1	0	0	0	0
+4 °C – Halved	43.6	27.3	11.5	202,480	16,912
+4 °C – Normal	13.9	50.6	15.6	597,040	37,408
+4 °C – Doubled	0.5	9.5	16.5	1,121,176	63,273

¹Average hectares per decade

4 Increased flammability of tundra Based on fire data and anecdotal evidence, tundra vegetation on the Seward Peninsula may be more flammable (due to the presence and abundance of lichen) than spruce forest. We explored this hypothesis by doubling the flammability of tundra and correspondingly reducing the probability of fires spreading (in all vegetation types). This increased the area burned in tundra and reduced the area of spruce forest burned (originally the most flammable vegetation type). However, we were then unable to match the model output to both the observed fire record and the vegetation distribution. If we calibrate the model to match the observed fire regime with high tundra flammability, the resultant landscape contains much more spruce than observed currently. If we calibrate the model to match the vegetation, we cannot match the fire record. This sensitivity analysis of model assumptions suggests that, if lichen-dominated tundra is more flammable than spruce forest, there is less spruce and/or more fires on the current landscape than if fire and vegetation were in equilibrium with climate. This situation might result from deforestation by gold miners 100 years ago and/or increased human ignitions in recent decades.

Discussion

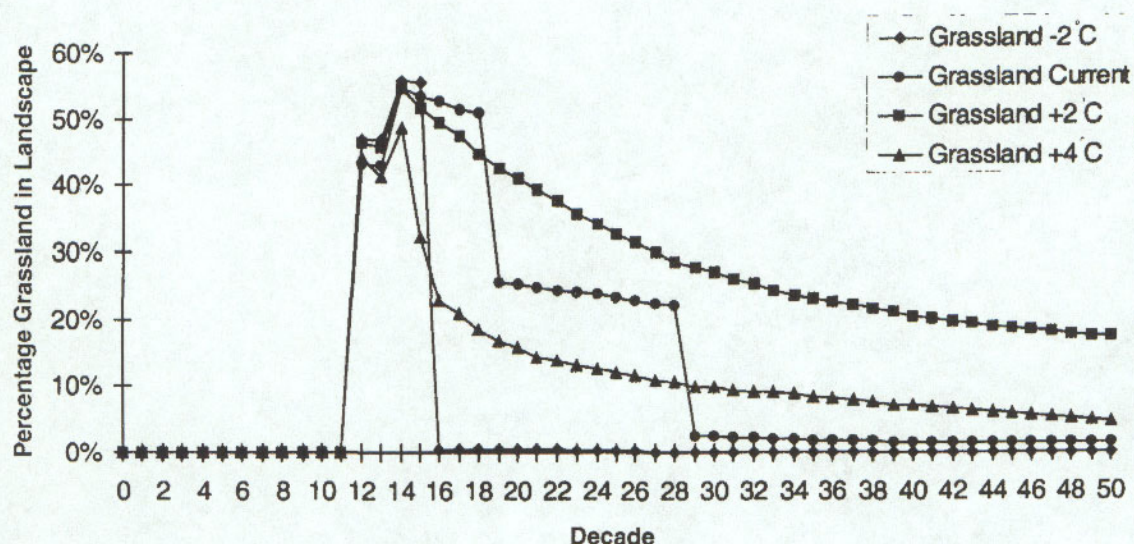
Our simulations suggest that a climatic warming of as little as 2 °C would cause substantial conversion from tundra to forest on the Seward Peninsula. Under the 2 °C warming scenarios (both instantaneous and ramped) there was a time lag for the doubling of the initial total forest cover of 70–290 y, which is similar to time-lag estimates of treeline movement from pollen cores 3500–5000 y ago (MacDonald *et al.* 1993). Furthermore, spruce

forest migration (both in-filling and colonization that doubled the initial spruce forest cover) had a time lag of 150–500 y. These changes would have important regional implications for future carbon budgets and biotic feedbacks to climate. Such time-lags in forest advance would likely result in tundra being exposed to warmer temperatures than at present before being replaced by forest, which might cause transient loss of stored carbon from tundra (Smith & Shugart 1993) that would not be predicted by equilibrium simulation models (King & Neilson 1992; Oechel *et al.* 1993; Smith & Shugart 1993; Chapin & Starfield 1997).

The boreal forest, which contains 11% of the world's soil carbon (Post *et al.* 1982) and 40% of the world's reactive soil carbon (McGuire *et al.* 1995), would likely serve as a major carbon source in light of the increases in fire number and area burned simulated by ALFRESCO (Kasischke *et al.* 1995, Kurz & Apps 1995). White spruce forest migration in as little as 150 years would reduce albedo in areas previously treeless (i.e. tundra) by converting white snow-covered tundra to a darker spruce forest. The resulting increase in absorbed radiation would lead to positive feedbacks to climatic warming (Bonan *et al.* 1992, 1995; Foley *et al.* 1994).

Spatial processes such as fire spread and seed dispersal can cause substantial changes in vegetation distribution and pattern. By decreasing the ignition and increasing the fire spread probabilities we were able to simulate the average fire number and size that have been observed on the Seward Peninsula over the past 50 years (Kasischke & French 1997). The changes in the climate sensitivity of fire ignition and spread (compared to the original simulation runs) that were required to match the observed fire regime indicate that fire spread and fire size are much more responsive to climatic warming than

(a)



(b)

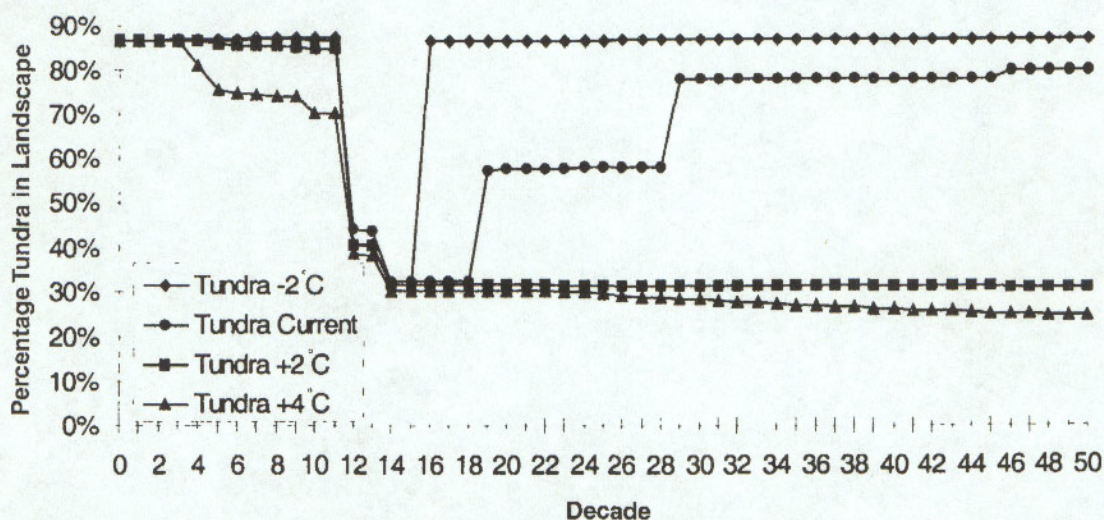


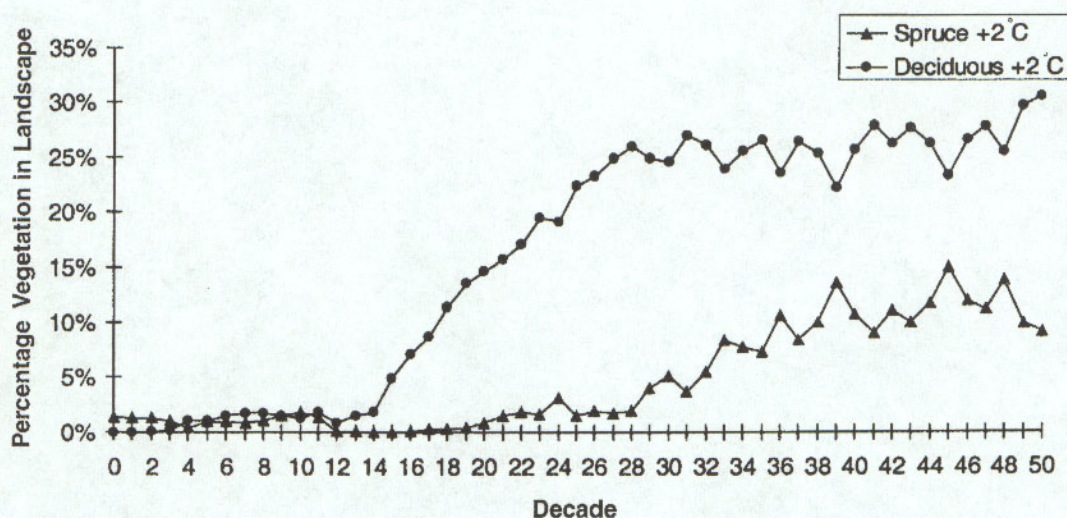
Fig. 5 Average percentage vegetation cover across the landscape for (a) grassland cover and (b) tundra cover, for expt 9 (see Table 2). Results for instantaneous -2°C (diamonds), $+2^{\circ}\text{C}$ (squares), $+4^{\circ}\text{C}$ (triangles), and current climate (circles) scenarios. Drought event occurred from decade 11 through 14. Simulated for 500 y and replicated 100 times.

are ignition and fire number (Gardner *et al.* 1996; Skinner *et al.* in press).

The large increase in the proportion of deciduous forest in the warmer climate is consistent with widespread dominance of poplars during the Holocene thermal maximum 9000 y bp (Brubaker *et al.* 1995), which contrasts with spruce dominance during cooler periods. Spruce and poplar currently co-occur across a broad

climate gradient, so we suggest that changes in fire regime may have been primarily responsible for past changes in spruce or deciduous dominance in Alaskan forests. Our results clearly indicate that fire regime (i.e. frequency and size of fires) plays an important role in determining the relative abundance of ecosystem types and may cause qualitatively different patterns across the landscape.

(a)



(b)

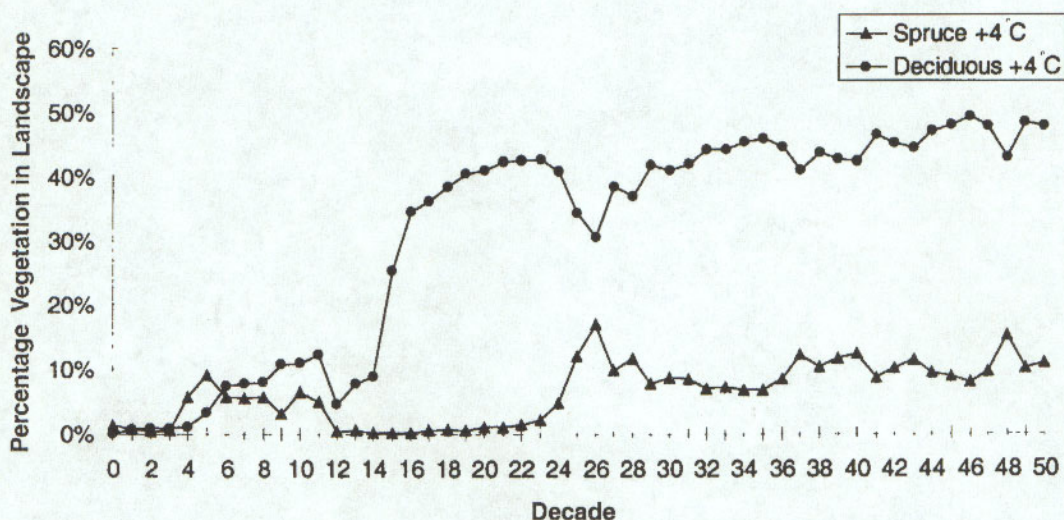


Fig. 6 Average percentage cover of tundra (squares), white spruce forest (triangles), deciduous forest (circles), and grassland (diamonds) across the landscape, under climate scenarios of (a) instantaneous +2°C and (b) instantaneous +4°C, with a 40-y drought event (from decade 11 through 14). Simulated for 500 y and replicated 100 times.

Transient events can cause long-term changes in vegetation distribution and disturbance regime, creating historical legacies that cannot be explained by current climate (Ritchie 1986). The simulation of short-term extremes in temperature and precipitation caused the establishment and persistence of drought-resistant grassland–steppe vegetation that is currently absent from the Alaskan boreal forest except in dry microsites (Lloyd *et al.* 1994) and regions (Hogg & Hurdle 1995). The high

flammability of this vegetation type resulted in fires that repeatedly burned and maintained the grassland but also occasionally spread into adjacent less flammable vegetation, causing much more widespread landscape conversion to grassland (49–56%) than we had previously simulated using a nonspatial model (18%) (Chapin & Starfield 1997). Biogeochemical models also simulate reduced forest cover with increased temperature scenarios (VEMAP 1995). Field observations indicate that, once

established, grasslands are surprisingly stable as a result of fire-vegetation and herbivore-vegetation feedbacks (D'Antonio & Vitousek 1992). For example, in the NE Siberian boreal forest, grasslands that were created near villages have remained as grassland for more than 100 years after villages were abandoned (S. A. Zimov & F. S. Chapin, unpubl. obs.). Conversion of tundra to grassland-steppe could plausibly occur over broad areas, under GCM-predicted scenarios of drier growing season climates (Chapin & Starfield 1997). This hypothesis is consistent with the palaeoecological literature, which repeatedly demonstrates the development of new ecosystems or novel combinations of species following climatic change (Davis 1981, Chapin & Starfield 1997).

The major results of our simulations are that: (i) a warming climate (as little as 2°C) will lead to a conversion of tundra to white spruce and deciduous forest on the Seward Peninsula; (ii) regardless of the rate or magnitude of warming, vegetation will continue to change for centuries following climatic change; and (iii) specific transient events can influence long-term rates and patterns of vegetation change and disturbance leading to 'legacies' that cannot be explained by current climate. These results suggest that transient vegetation changes influence both the rate and endpoint of vegetation change in ways that have important regional implications for both carbon storage and biotic feedbacks to climate. These results highlight the importance of developing spatially explicit transient models of vegetation change at the landscape and regional scales to perform 'thought experiments'. These experiments enable us to look for consistencies and inconsistencies between the current landscape pattern, the historical record (to the extent it exists), and our understanding of key processes on the landscape, and then project forward to look for both unexpected possibilities and robust conclusions.

Acknowledgements

We thank an anonymous reviewer and Dr Chris Field, Subject Editor of *Global Change Biology*, for their constructive comments. This research was supported by NSF grants as components of Arctic System Science (OPP-9630913 and OPP-9318532) and the Bonanza Creek LTER program (DEB-9211769 and DEB-9810217). A detailed description of the spatial model is also available on the Bonanza Creek LTER World Wide Web server at <http://www.lter.alaska.edu/pubs/alfresco.html>.

References

- Bliss LC, Matveyeva NV (1992) Circumpolar arctic vegetation. In *Arctic Ecosystems in a Changing Climate: an Ecophysiological Perspective* (eds Chapin FS III et al.), pp 59–89. Academic Press, San Diego, CA.
- Bonan GB, Chapin FS III, Thompson SL (1995) Boreal forest and tundra ecosystems as components of the climate system. *Climatic Change*, **29**, 145–167.
- Bonan GB, Pollard D, Thompson SL (1992) Effects of boreal forest vegetation on global climate. *Nature*, **359**, 716–718.
- Brubaker LB, Anderson PM, Hu FS (1995) Arctic tundra biodiversity: A temporal perspective from late Quaternary pollen records. In *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences* (eds Chapin FS III, Körner C), pp 111–125. Springer, Berlin.
- Chalita S, Le Treut H (1994) The albedo of temperate and boreal forest and the northern hemisphere climate: a sensitivity experiment using the LMD GCM. *Climate Dynamics*, **10**, 231–240.
- Chapin FS III, Starfield AM (1997) Time lags and novel ecosystems in response to transient climatic change in arctic Alaska. *Climatic Change*, **35**, 449–461.
- Charney JG, Quirk WJ, Chow SH, Kornfeld J (1977) A comparative study of effects of albedo change on drought in semiarid regions. *Journal of Atmospheric Science*, **34**, 1366–1385.
- Clark JS (1988) Effect of climate change on fire regimes in northwestern Minnesota. *Nature*, **334**, 233–235.
- Dale VH (1997) The relationship between land-use change and climate change. *Ecological Applications*, **7**, 753–769.
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass-fire cycle, and global change. *Annual Review of Ecology and Systematics*, **23**, 63–87.
- Davis MB (1981) Quaternary history and the stability of forest communities. In: *Forest Succession: Concepts and Application* (eds West DC et al.), pp 132–153. Springer, New York.
- ESRI (1994) ARCDoc, Version 7.0. On-line Documentation for ARC/INFO Geographic Information Software. Environmental Systems Research Institute, Redlands, CA.
- Fastie CL (1995) Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology*, **76**, 1899–1916.
- Flannigan MD, Harrington JB (1988) A study of the relation of meteorological variables to monthly provincial area burned by wildfire in Canada (1935–80). *Journal of Applied Meteorology*, **27**, 441–452.
- Flannigan MDF, Van Wagner CE (1991) Climate change and wildfire in Canada. *Canadian Journal of Forest Research*, **21**, 66–72.
- Flannigan MDF, Bergeron Y, Engelmark O, Wotton BM (1998) Future wildfire in circumboreal forests in relation to global warming. *Journal of Vegetation Science*, **9**, 469–476.
- Fleming MD (1997) *Alaska Vegetation/Land Cover Classes*. U.S. Geological Survey Global Change Program, Land Data Systems — Arctic Land Process Studies, <http://agdc.usgs.gov/data/projects/hlct/hlct.html>.
- Foley JA, Kutzbach JE, Coe MT, Levis S (1994) Feedbacks between climate and boreal forests during the Holocene epoch. *Nature*, **371**, 52–54.
- Gardner RH, Romme WH, Turner MG (1999) Predicting forest fire effects at landscape scales. In *Spatial Modeling of Forest Ecosystems* (eds Mladenoff DJ, Baker WL), pp 163–185. Cambridge University Press, Cambridge.
- Gardner RH, Hargrove WW, Turner MG, Romme WH (1996) Global change, disturbances and landscape dynamics. In *Global Change and Terrestrial Ecosystems* (eds Walker B, Steffen W), 149–172. Cambridge University Press, Cambridge.

- Hammond T, Yarie J (1996) Spatial prediction of climatic state factor regions in Alaska *Ecoscience*, **3**, 490–501.
- Haugen RK (1982) Climate of remote areas in north-central Alaska 1975–1979 summary. In: *US Army Cold Regions Research and Engineering Laboratory Report* 82–351–114
- Hobbie SE, Chapin FS III (1998) The response of tundra plant biomass, aboveground production, nitrogen, and CO₂ flux to experimental warming *Ecology*, **79**, 1526–1544
- Hogg EH, Hurdle PA (1995) The aspen parkland in western Canada: a dry-climate analogue for the future boreal forest? In: *Boreal Forests and Global Change* (eds Apps MJ, Price DT), 391–400. Kluwer, Dordrecht
- Holling CS (1992) The role of forest insects in structuring the boreal landscape. In: *A Systems Analysis of the Global Boreal Forest* (eds Shugart HH *et al.*), pp. 170–191. Cambridge University Press, Cambridge
- Hopkins DM, Matthews JV, Schweger CE, Young SB (1982) *Paleoecology of Beringia*. Academic Press, New York
- Kasischke ES, Christensen NL, Stocks BJ (1995) Fire, global warming, and the carbon balance of boreal forests *Ecological Applications*, **10**, 2941–2951
- Kasischke ES, French NHF (1997) Constraints on using AVHRR composite index imagery to study patterns of vegetation cover in boreal forests *International Journal of Remote Sensing*, **18**, 2403–2426.
- King GA, Neilson RP (1992) The transient response of vegetation to climate change: a potential source of CO₂ to the atmosphere *Water, Air, and Soil Pollution*, **64**, 365–383
- Kurz WA, Apps MJ (1995) An analysis of future carbon budgets of Canadian boreal forests *Water, Air, and Soil Pollution*, **82**, 321–331
- Lloyd AH, Armbruster WS, Edwards ME (1994) Ecology of a steppe-tundra gradient in interior Alaska *Journal of Vegetation Science*, **5**, 897–912
- MacDonald GM, Edwards TWD, Moser KA, Pienitz R, Smol JP (1993) Rapid response of treeline vegetation and lakes to past climate warming *Nature*, **361**, 243–246
- Mattson WJ, Haack RA (1987) The role of drought in outbreaks of plant-eating insects *Bioscience*, **37**, 110–118.
- Maxwell B (1992) Arctic climate potential for change under global warming. In: *Arctic Ecosystems in a Changing Climate: an Ecophysiological Perspective* (eds Chapin FS III *et al.*), pp. 11–34. Academic Press, San Diego, CA
- McGuire AD, Melillo JW, Kicklighter DW, Joyce LA (1995) Equilibrium responses of soil carbon to climate change: empirical and process-based estimates *Journal of Biogeography*, **22**, 785–796
- Neilson RP (1993) Transient ecotone response to climatic change: some conceptual and modeling approaches *Ecological Applications*, **3**, 385–395
- Noble IR (1993) A model of the responses of ecotones to climate change *Ecological Applications*, **3**, 396–403
- Oechel WC, Hastings SJ, Vourlitis G, Jenkins M, Reichers G, Grulke N (1993) Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source *Nature*, **361**, 520–523
- Pastor J, Post WM (1986) Influence of climate, soil moisture, and succession of forest carbon and nitrogen cycles *Biogeochemistry*, **2**, 3–27
- Pastor J, Post WM (1988) Responses of northern forests to CO₂-induced climate change. *Nature*, **334**, 55–58
- Payette S (1983) The forest tundra and present tree-lines of the northern Quebec-Labrador Peninsula. In: *Tree-Line Ecology: Proceedings of the northern Quebec Tree-Line Conference* (eds Morisset P, Payette S), pp. 3–23. University Laval, Quebec.
- Pielke RA, Vidale PL (1996) The boreal forest and the polar front *Journal of Geophysical Research-Atmospheres*, **100**, 25755–25758.
- Post WM, Emanuel WR, Zinke PJ, Stangenberger AG (1982) Soil carbon pools and world life zones *Nature*, **298**, 156–159
- Prentice KC, Fung IY (1990) The sensitivity of terrestrial carbon storage to climate change *Nature*, **346**, 48–51
- Reap RM (1991) Climatological characteristics and objective prediction of thunderstorms over Alaska *Weather and Forecasting*, **6**, 309–319
- Ritchie JC (1986) Climate change and vegetation response *Vegetatio*, **67**, 65–74
- Rupp TS, Starfield AM, Chapin FS III (2000) A frame-based spatially explicit model of subarctic vegetation response to climatic change: comparison with a point model *Landscape Ecology*, **15**, 383–400
- Serreze MC, Walsh JE, Chapin FS III (in press) Observational evidence of recent change in the northern high-latitude environment *Climatic Change*, in press
- Shugart HH, West DC (1980) Forest succession models *Bioscience*, **30**, 308–313.
- Sirois L, Bonan GB, Shugart HH (1994) Development of a simulation model of the forest-tundra transition zone of northeastern Canada *Canadian Journal of Forest Research*, **24**, 697–706.
- Skinner WR, Stocks BJ, Martell DL, Bonsal B, Shabbar A (in press) The association between circulation anomalies in the mid-troposphere and area burned by wildland fire in Canada *Theoretical and Applied Climatology*, in press
- Smith TM, Shugart HH (1993) The transient response of terrestrial carbon storage to a perturbed climate *Nature*, **361**, 523–526
- Solomon AM (1992) The nature and distribution of past, present and future boreal forests: lessons for a research and modeling agenda. In: *A Systems Analysis of the Global Boreal Forest* (eds Shugart HH *et al.*), pp. 170–191. Cambridge University Press, Cambridge
- Starfield AM (1991) Qualitative rule-based modeling *Bioscience*, **40**, 601–604
- Starfield AM, Chapin FS III (1996) Model of transient changes in arctic and boreal vegetation in response to climate and land use change. *Ecological Applications*, **6**, 842–864
- Starfield AM, Cummings DHM, Taylor RD, Quadling MS (1993) A frame-based paradigm for dynamic ecosystem models *AI Applications*, **7**, 1–13.
- Stocks BJ (1991) The extent and impact of forest fires in northern circumpolar countries. In: *Global Biomass Burning: Atmospheric, Climatic and Biospheric Implications* (ed. Levine JL), 197–202. MIT Press, Cambridge, USA
- Thomas G, Rowntree PR (1992) The boreal forests and climate *Quarterly Journal of the Royal Meteorological Society*, **118**, 469–497
- Thornwaite CW, Mather JR (1957) Instructions and tables for computing potential evaporation and the water balance. *Publications in Climatology*, **10**, 183–311
- Trigg WM (1971) *Fire Season Climatic Zones of Mainland Alaska*. US Department of Agriculture, Portland, USA.

- Turner MG, Hargrove WH, Gardner RH, Romme WH (1994) Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *Journal of Vegetation Science*, **5**, 731–742.
- Turner MG, Romme WH, Gardner RH, Hargrove WW (1997) Effects of fire size and pattern on early post-fire succession in subalpine forests of Yellowstone National Park, Wyoming. *Ecological Monographs*, **67**, 411–433.
- USGS (1990) *Digital Elevation Models Data Users Guide 5* US Department of the Interior, US Geological Survey, Reston, VA.
- Van Cleve K, Chapin FS III, Dyrness CT, Viereck LA (1991) Element cycling in taiga forests: State-factor control. *Bioscience*, **41**, 78–88.
- VEMAP (1995) Vegetation/ecosystem modeling and analysis project: Comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO₂ doubling. *Global Biogeochemical Cycles*, **4**, 407–437.
- Viereck LA (1973) Wildfire in the boreal forest of Alaska. *Quaternary Research*, **3**, 465–495.
- Yurtsev BA (1982) Relics of the xerophyte vegetation of Beringia in northeastern Asia. In *Paleoecology of Beringia* (eds Hopkins DM *et al.*), pp 157–177. Academic Press, New York.
- Zimov SA, Chuprynin VI, Oreshko AP, Chapin FS III, Reynolds JF, Chapin MC (1995) Steppe-tundra transition: an herbivore-driven biome shift at the end of the Pleistocene. *American Naturalist*, **146**, 765–794.